Establishment of different riparian plant communities from the same soil seed bank

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Chapter 1

General introduction

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Description and threats of riparian plant communities

Banks of rivers and lakes in large parts of the world are, under natural conditions, covered with herbaceous vegetation consisting of mudflat pioneers, helophytes/emergents and reed beds. These 'riparian' plant communities are, following the definition of Looijen and Van Andel (1999): the set of individuals of two or more plant species that occur in the intersection of the areas occupied by populations of these species. The species richness of these communities can be high and they have a high nature conservation interest (Van der Valk, 2005; Verdonschot et al., 2012; Verhoeven, 2014). Mudflat pioneer communities depend on areas with bare mud that fall dry during summer, as a result of seasonal water-level fluctuations (Jans and Drost, 1995; Nijhof, 2002). These communities contain annual or biennial species such as *Senecio congestus*, *Chenopodium rubrum* and *Rumex maritimus*. Such species produce lots of seeds, which is an important food source for waterfowl. Helophyte communities in shallow water are dominated by tall emergent species, such as *Typha latifolia* and *Phragmites australis*. They are an important habitat for all kinds of fauna: birds, fish, mammals and macro-invertebrates. Helophyte communities are able to establish in shallow water, but large-scale establishment takes place on bare mudflats (Clevering and Van Gulik, 1997; Lenssen et al., 1999; Coops et al., 1999). Reed beds above the waterline that are periodically flooded often are dominated by *Phragmites australis* (Lenssen, 1998).

Riparian plant communities are threatened or have largely disappeared due to agricultural land use, urbanization and climate change (Verdonschot et al., 2012; Verhoeven, 2014). Agricultural use and urbanization often result in fixed water levels. Therefore mudflats are absent or rare and pioneer and helophyte communities cannot establish (Jans and Drost, 1995; Clevering and Van Gulik, 1997; Coops et al., 1999; Lenssen et al., 1999; Sollie and Verhoeven, 2008). Steep or hard-facing banks along channels and ditches or embankments of lakes and rivers also prevent large-scale establishment of riparian plant communities (Boedeltje et al., 2003A; Everaert et al., 2013). High numbers of herbivores, such as cattle, geese and musk rats graze heavily on riparian communities (Van den Wyngaert et al., 2003; Sollie and Verhoeven, 2008; Dingemans et al., 2011; Veen et al., 2013; Sarneel et al., 2014). Eutrophication due to agricultural land use and urbanization results in increased turbidity, which decreases the possibility for helophyte species to establish under water (Clevering et al., 1996; Sarneel et al., 2011). Moreover, eutrophication leads to an increase of litter or soil organic matter, reducing the germination of plant species (Lenssen et al., 1999; Lenssen et al., 2000; Blomqvist, 2005). The growing intensity of agricultural land use requires intensive mowing of helophyte communities and reed beds to keep channels and ditches open (Best, 1993; Huijser et al., 2001; Blomqvist et al., 2003). Waterboards have noticed that climate change already leads to an increase of eutrophicated runoff during summer and, therefore, an increasing need to mow channels and ditches (Ter Heerdt, personal observation).

Restoration of riparian communities and the need to understand how riparian plant communities are assembled

In many wetlands measures are taken to restore and maintain riparian plant communities. Examples are available from North America (Van der Valk, 2005), China (Wang et al., 2008; Hong et al., 2012) and from Western Europe (Coops et al., 2004; Verdonschot et al., 2012). In Europe legislation has been developed in order to maintain and restore aquatic ecosystems and their riparian communities. The Water Framework Directive (WFD; European Commission, 2000) demands the restoration of helophyte and reed bed communities. Natura 2000, especially the Birds Directive (European Commission, 2009), demands the maintenance and restoration of riparian communities for birdlife. Therefore waterboards in the Netherlands are planning to restore 4000–8000 km of riparian communities (Ligtvoet et al., 2008). Target communities vary from reed beds to mudflat pioneer communities (Vulink and Van Eerden, 1998; Nijhof, 2002; Coops et al., 2004). The most important measures waterboards can take are reintroducing natural water-level fluctuation and drawdowns to restore the zone of bare mud that riparian communities need to become established (Vulink and Van Eerden, 1998; Coops and Hosper, 2002; Sarneel et al., 2014). A second important measure is (re)construction of gently sloped banks to replace steep or hard facing banks (Boedeltje et al., 2003 A; Everaert et al., 2013). Further, creating floodplain flats (Nienhuis et al., 2002; Nijhof, 2002) and removal of vegetation and topsoil (Lenssen et al., 1999; Blomqvist, 2005), is being carried out to create space for riparian communities.

However, attempts to restore riparian plant communities are not always successful. Too often the goals of the European Water Framework Directive and Natura 2000 are not reached: helophyte stands do not establish along lakes and channels, target species remain absent in fen riparian zones, and species richness remains low. The cause of these failures is not well understood (Ozinga, 2008; Sarneel, 2010; Lamers et al., 2014; González et al., 2015). The results of fluctuating water-level management and drawdowns strongly depend on the drawdown date. However, the most appropriate drawdown date depends on the target-community and local weather conditions, and has to be determined by trial and error (Fredrickson, 1991; Wenzel and Shaw, 2014). Everaert et al. (2013) concluded that it is difficult to give conclusive advice on the most efficient water-level management and that the design of gently sloped banks is an important factor for its success. Moreover, due to climate change, temperature is rising, and both very wet and very dry periods will be more common in Western Europe (Klein Tank and Wenderink, 2009; Bakker and Bessembinder, 2012; Franken et al., 2013). This might affect the establishment of riparian communities negatively (Abrahams, 2008; Walck et al., 2011). Therefore, the European Water Framework Directive asks waterboards to take measures to mitigate the effect of climate change (European Commission, 2000; Verdonschot et al., 2012). Most likely the optimal drawdown date will change and an adapted water-level management will be needed to compensate for dry periods. To optimize water-level management, drawdown date and design of gently sloped banks requires a better understanding and predicting of the ecological processes that lead to the assembly of riparian plant communities (Ozinga et al., 2005; Lamers et al., 2014; Verhoeven, 2014).

Predicting the establishment of riparian communities from the soil seed bank

Most measures to restore riparian communities initially result in bare soil and the vegetation on restored banks is supposed to start from relic soil seed banks (Van der Valk and Pederson, 1989; Van der Valk et al., 1992; Boedeltje et al., 2003A). Alternatively, plant communities may establish from propagules that are dispersed by wind (Soons, 2006), water (Boedeltje et al., 2003B, 2004; Van den Broek et al., 2005; Van Leeuwen et al., 2014), waterfowl (Mueller and Van der Valk, 2002; Soons et al., 2008; Figuerola et al., 2010; Van Leeuwen et al., 2012), mammals (Stroh et al., 2012) or fish (Boedeltje et al., 2015; Van Leeuwen et al., 2015). To predict the success of restoration measures the species composition of the soil seed bank is often used. Riparian plant species are supposed to germinate and establish when bare soil or sediment is exposed to air (Van der Valk, 1981; Van der Valk and Welling, 1988; Weiher and Keddy, 1995). However, species that are abundant in the soil seed bank do not always establish in the pioneer plant community or establish every year, while species that are scarce in the soil seed bank may become abundant in the vegetation (Welling et al., 1988; Leck and Simpson, 1995; Brown, 1998; Hopfensperger, 2007). The failure of target species to establish or the unexpected appearance of non-target species can be the reason why restoration measures do not meet their goals. Therefore there is a need to understand the discrepancy between the soil seed bank and the vegetation that establishes from it.

The first explanation of the difference between soil seed bank and vegetation could be that the seed bank study was not sufficiently adequate to detect all species present. Two groups of methods are available to determine the composition of a soil seed bank: seed separation methods and seedling emergence methods (Roberts, 1981). Both groups of methods are laborious. Seed separation methods also detect non-viable or dormant seed that will not appear in the community, and thus tend to overestimate the number of species and seeds. Seedling emergence methods may underestimate the number of seeds, especially seeds of species that require certain germination conditions. Seed separation methods require a lot of washing, sieving, or flotation, and always need time consuming hand sorting. Seedling emergence methods require greenhouse space, frequent watering and seedling emergence may take months. Therefore, before attempts are made to predict which riparian communities might establish from the soil seed bank, a suitable method to determine the composition of the soil seed bank has to be found (Roberts, 1981).

Predicting the establishment of riparian communities based on the soil seed bank, environmental conditions and plant traits

The second explanation for the difference between soil seed bank and vegetation could be that not all viable seeds in the soil seed bank germinated, emerged or survived and therefore do not appear in the plant community. Predicting the composition of a plant community under given circumstances should be possible, because plant communities are not random selections of species. A community can appear repeatedly in place and time, depending on environmental conditions and the composition of the soil seed bank. Apparently there are 'community assembly rules' determining which species will enter a community and which will not (Diamond, 1975; Weiher and Keddy, 1999; Temperton et al., 2004). There are two groups of processes that shape the composition of plant communities. In the first group processes around the dispersal of seeds are the main limiting factors. These processes determine the composition of the soil seed bank. The second group concerns 'niche based' processes linked with the suitability of the local environment are limiting (Ozinga et al., 2005). In the latter case it will be the combination of processes (such as germination, growth, competition), environmental conditions (abiotic and biotic) and functional traits of plants species (such as stress tolerance, resistance to disturbance and competitive ability) that makes if a species can enter a community or not. Each process thus can behave as a sieve or filter through which only species can pass with functional traits that match the environmental conditions (Van der Valk, 1981; Keddy, 1992; Weiher and Keddy, 1995A). The general community assembly rules can be formulated as: a species can and will only enter a community when its functional traits allow it to pass all environmental filters. These community assembly rules can be used to unify studies of restoration, where predictions are based on key environmental conditions and the responses of species to them (Keddy, 1999).

The assembly of wetland plant communities has been studied for decennia and several models that use community assembly rules are available. They all show that different communities can establish from the same seed bank under different environmental conditions when the plant species have different traits and responses to these environmental conditions. Van der Valk's (1981) first model describes mainly the selection between submerged and emergent communities. The wetland can have two conditions: flooded and drawn down. Only plant species with traits that enable them to germinate when there is standing water will establish under flooded conditions. Species that have traits that enable them to germinate without standing water will establish after a drawdown. It is assumed in the model that competition will not result in the extirpation of any species from a wetland (Van der Valk, 1981). Moreover this model does not predict different possible communities to establish after a drawdown.

The second generation models are more complex. Van der Valk and Welling (1988) included more processes that affect the assembly of plant communities: seed germination, seedling survival, adult survival and competition (Fig. 1.1). This model is able to predict different communities to establish from a similar soil seed bank after a drawdown, depending on the environmental conditions and the traits of the different species. In this model competition can play an important role, leading to the extirpation of species.

Weiher and Keddy (1995) improved the model further. They tested 24 treatments for five years. Four environmental filters (seedling establishment, establishment in presence or absence of standing water, growth with time and competition and growth on nutrient-poor and nutrient-rich soil) resulted in four significantly different communities establishing from the same seed bank. The model was presented as a series of filters (Fig. 1.2).

To predict the effects of restoration measures and climate change, the advanced model of Weiher and Keddy (1995) seems to be the most appropriate. To use it, first the composition of the soil seed bank should be known. Secondly it should be decided which environmental conditions of filters could be relevant. Thirdly the functional traits of the plant species in relation to these filters should be known. In some cases these traits can be found in literature and databases. If not available, a series of experiments is needed.

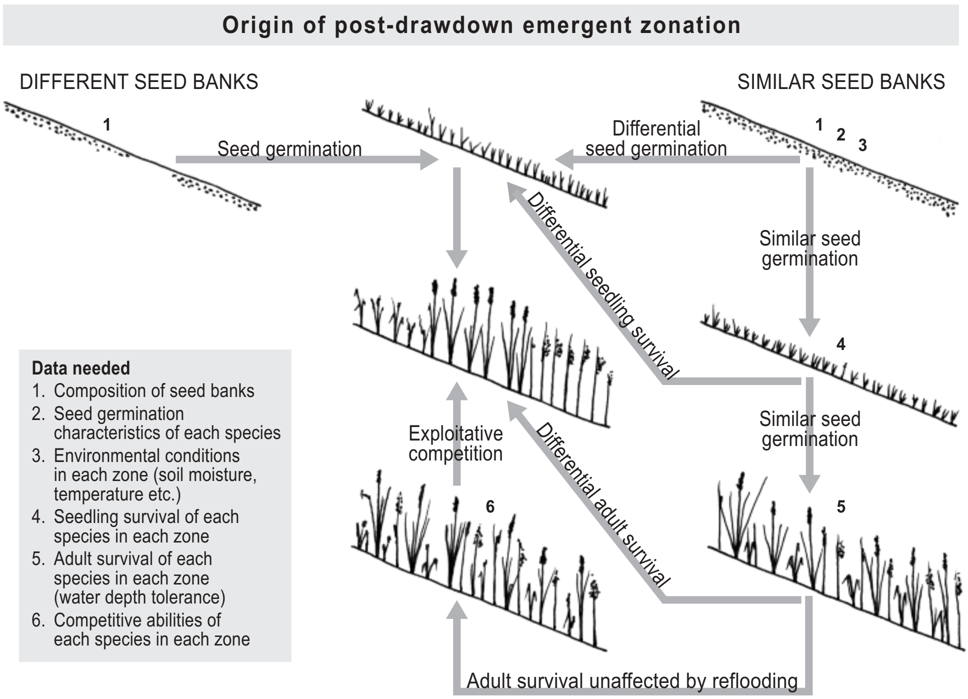

Figure 1.1 Potential pathways leading to the development of an emergent range of communities on a gently sloped bank in a non-tidal, freshwater wetland after drawdown (after Van der Valk and Welling, 1988).

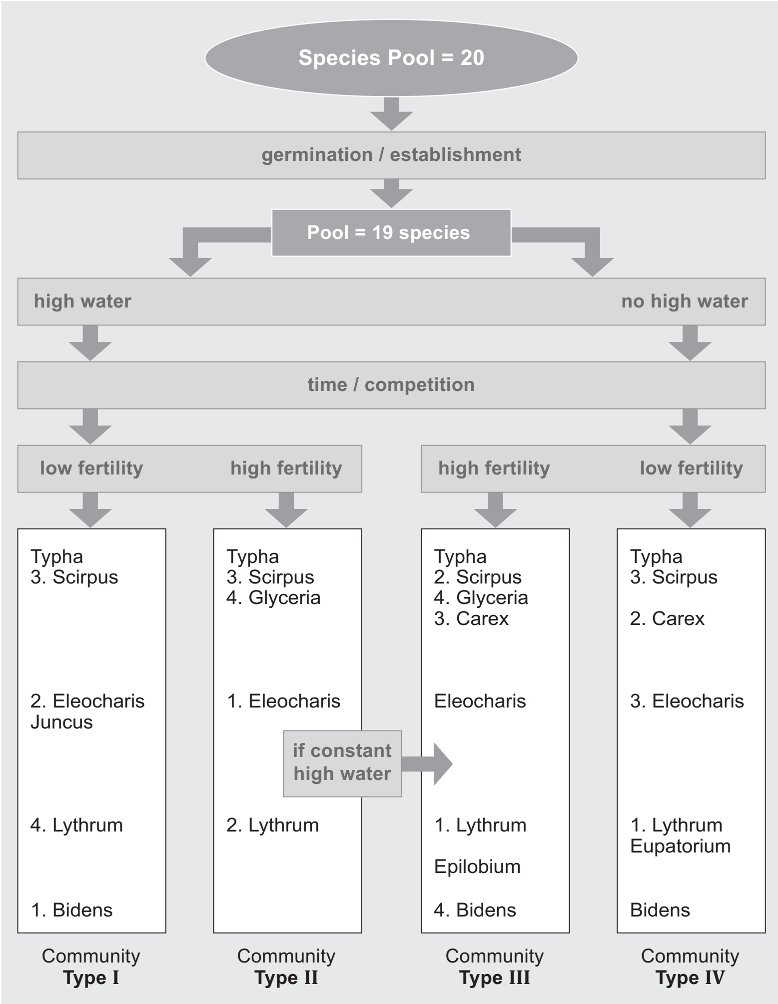

Figure 1.2 Community assembly model (from the results of community ordination). Horizontal bands represent a series of "environmental filters". Numbers next to the final community types correspond to mean rank abundance (after Weiher and Keddy, 1995).

The Oostvaardersplassen drawdown as a test case

To test if the model of Weiher and Keddy (1995) based on knowledge of the soil seed bank and a series of community assembly rules, enable waterboards to predict the result of their restoration measures sufficiently accurate, I used the drawdown in the Oostvaardersplassen as a test case. During this drawdown, vegetation development and environmental conditions have been well documented. To optimize drawdowns as a management tool in the future, the manager of the lake, the former Ministry of Transport, Public Works and Water Management, commissioned further studies. The Oostvaardersplassen nature reserve in the Netherlands (52°26’N, 5°19’E) is with 3600 ha of marshland one of the largest freshwater marshes in northwestern Europe (Vulink and Van Eerden, 1998). Due to a combination of high grazing pressure by Greylag geese (*Anser anser*) most of the helophyte communities with *Phragmites australis* and *Typha latifolia* disappeared. As the water level hardly fluctuated, mudflats with annual and biennial species became scarce and helophytes were not able to reestablish (Wigbels, 1990; Vulink and Van Eerden, 1998; Beemster et al., 2010). In order to enable the reestablishment of helophytes, the water level in the western part of the lake (2100 ha) was lowered from 1987 to 1988 and remained dry until 1991. Expected was that a large area would be colonized by a *Typha latifolia* dominated community. However this prediction did not become true as only 1–2% of the area became dominated by *Typha latifolia* and several different mudflat communities with *Senecio congestus*, *Chenopodium rubrum* and *Rumex maritimus* in different proportions became wide spread instead (Jans and Drost, 1996; Vulink and Van Eerden, 1998). To understand what had happened, a soil seed bank study was initiated in an undisturbed part of the lake that has not been subject to a drawdown, to determine the abundance of *Typha latifolia* and other riparian species. First, this question required a series of preliminary tests to determine which method would be suitable to determine the soil seed bank in this wetland.

Second, a series of experiments was carried out to find the community assembly rules that determine the establishment of the species from the soil seed bank in the Oostvaardersplassen. During the period that the water level dropped, 1987–1988, the weather conditions (temperature, precipitation and evaporation) were monitored. It seemed that vegetation development depended on different weather conditions during the early establishment of each community. A community dominated by *Typha latifolia* established during a wet and cool period. *Chenopodium rubrum* and *Rumex maritimus* were the most abundant species after a very dry and hot period. *Senecio congestus* became dominant when after a very dry and hot period the weather became very wet and warm. Presence of *Phragmites australis* seemed to be independent of the weather conditions and this species spread vegetative during the second year of drawdown where *Typha latifolia* did not. Therefore, temperature and soil moisture conditions, as a result of various weather conditions, were potential key factors. Based on the models of Van der Valk and Welling (1988) and Weiher and Keddy (1995) these conditions could determine germination and seedling emergence, but also adult growth. Competition also was likely to be a potential filter, as the soil was nutrient rich and many of the species that established could reach a high yield. The five species mentioned above were the key species to test.

Fluctuating water-level management, drawdowns and the restoration of floodplains are planned in areas with different soil types than in Oostvaardersplassen; varying from nutrient-rich ripened clay to nutrient-poor Pleistocene sand (Coops and Hosper, 2002; Nienhuis et al., 2002; Coops et al., 2004). After topsoil removal or the reconstruction of gently sloped banks and floodplains, soil type often will be Pleistocene sand, which is a common soil type in the Netherlands. Clay or sand may result in different effects of moisture conditions on seedling emergence and plant growth, because of containing different amounts of water (Van Zuidam et al., 2014). Therefore, I tested the establishment of *Typha latifolia* and *Phragmites australis* on these two soil types in a separate series of experiments.

With the outcome of the various experiments I will use the model of Weiher and Keddy (1995) to simulate which communities will establish under various conditions. As I tested the species response to conditions similar to the conditions during the 1987–1988 drawdown, the outcome should be comparable with the communities that established in the field. If it does, I will conclude that I have found the community assembly rules that determine the establishment of the species from the soil seed bank in the Oostvaardersplassen.

Towards management implications

Furthermore I want to make the results of this search applicable to predict the outcome of measures to restore riparian plant communities more in general. To do so, I will use the results from the previous chapters to determine a series of community assembly rules that describe the establishment of riparian plant communities, from bare soil towards the end of the first or second growing season. To test if these rules are workable I will use them to reconstruct the establishment of the plant communities during the test case of the Oostvaardersplassen drawdown. The number of species that can be tested will be limited. Therefore I also will explore the possibility to determine the response of riparian species to temperature and moisture, using functional groups and guilds. As becomes clear in this thesis, an effective prediction of the results of restoration measures requires knowledge of the future temperature and moisture conditions. These can be predicted based on historical weather data. Using the assembly rules that I defined and predictions of future environmental conditions, I will suggest the optimal drawdown date for various riparian communities in the Netherlands, improvements for the design of gently sloped banks and measures to mitigate climate change.

Thesis outline

A reliable determination of the composition of the soil seed bank is the basis of successful predictions of the success of restoration measures. Therefore in **chapter 2** I will search the literature for the most appropriate methods. These I will test experimentally with soil samples from wetlands with clay, peaty and sandy soils. When needed, I will improve methods to find the largest number of species and seeds with a minimum of effort.

When soil moisture conditions determine the amount of species and individuals that establish on bare soil, this will also affect the outcome of seed-bank analysis using a seedling emergence method. In **chapter 3** I focus on the amount of water that is needed to maximize germination and the kind of preliminary studies that could be needed before starting a large-scale soil seed-bank study.

In **chapter 4** the soil seed banks of different areas in the Oostvaardersplassen reserve will be described. I will estimate the number of seedlings per m^2 that can be expected to establish from these seed banks, based on Van der Valk's (1981) model. Which species will be able to establish under non-flooded conditions, will be determined based on their functional traits derived from literature. The resulting simulated communities should, potentially, be the riparian communities that establish in the tested areas after a drawdown. These simulated communities I will compare with the communities that actually established.

In **chapter 5** I will perform several experiments in climate chambers to test the response of riparian species to different temperature and moisture conditions and soil type. Important functional traits will be percentage seedling emergence and survival under various conditions. Main question will be if species respond differently and if different environmental conditions will result in the early establishment of different communities.

The effect of moisture conditions and soil type on adult growth and competition will be studied in **Box 1**. This requires several experiments in climate chambers and greenhouses. The yield of each species under various conditions in monoculture and the outcome of competition in a replacement experiment will be important traits. Again the main question will be if species respond differently and if different environmental conditions will result in the establishment of different communities.

In **chapter 6** I will synthesize the results of the earlier chapters. I will describe community assembly rules related to dispersal and niche-based assembly. With these rules I will simulate the assembly of the communities that established during the first year of drawdown in the Oostvaardersplassen. Further I will simulate the establishment of *Typha latifolia* and *Phragmites australis* on clay and sand under various environmental conditions during two growing seasons. The results of these simulations will be compared with the observations in the Oostvaardersplassen. If the simulations of the establishment of riparian plant communities match rather well with the field observations, the assembly rules that I will determine in this thesis can be used to determine the best drawdown date for the establishment of certain communities. This first requires a simulation of the weather conditions to be expected under current climate and after climate change. This simulation will be based on historical KNMI data, and data transformed with the KNMI Climate Explorer. Secondly I will couple the simulated biomass of the five species tested under various temperature and moisture conditions with the probability that these various environmental conditions might occur in the future. This way, I can estimate the probability that different riparian communities will establish. Finally I will use this information to advice on restoration measures such as drawdown date, topsoil removal date, the design of gently sloped banks and counteractions on effects of climate change.

Seedlings emerging from the soil seed bank. Photo Gerard Ter Heerdt.